Visceral vasculature in the family Cordylidae (Reptilia: Squamata)

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Major circulatory patterns in lizards of the family Cordylidae are poorly known, but may serve as a source of characters for systematics. Two specimens each of the cordylines, *Cordylus jordani* and *C. polyzonus*, and the gerrhosaurine, *Zonosaurus madagascariensis* were prepared by Microfil™ injection and whole body clearing and staining to serve as the basis for a comparison of cordylid visceral vasculature. The greatest amount of variation within the family is seen in the vessels of the hepatic portal system, whereas venous drainage and the arterial system (exclusive of the coeliac artery and its branches) are largely conservative within the group. Despite extensive homoplasy in lizards as a whole, cordylids (*sensu lato*), and especially gerrhosaurines, share a number of features of vasculature that support their sister-group relationship to the Scincidae. The proximity of the origin of the anterior and posterior mesenteric arteries stands as a putative synapomorphy of cordylines + gerrhosaurines. Features of the hepatic portal drainage may be autapomorphic for the genus *Cordylus* or for cordylines as a whole.

Oor die hoof bloedsomlooppatrone in akkedisse van die familie Cordylidae is weinig bekend, maar dit kan moontlik as 'n bron van sistematiese karakters dien. Twee eksemplare van elk van die cordylines, *Cordylus jordani* en *C. polyzonus*, en die gerrhosaurine, *Zonosaurus madagascariensis* is voorberei vir Microfil™ inspuiting, en heelliggaam-opheldering en -kleuring, om as die basis te dien vir 'n vergelyking van cordylide bloedvatstelsels. Die grootste variasie in die familie is in die vate van die lewerpoortsisteem, terwyl veneuse dreinering en die arteriestelsel hoofsaaklik konserwatief binne die groep voorkom. Ten spyte van uitgebreide homoplasie in akkedisse as geheel, deel cordylide (*sensu lato*), en veral gerrhosaurines, 'n aantal bloedvatkenmerke wat hulle suster-groepverwantskap met die Scincidae ondersteun. Die nabyheid van die oorsprong van die anterior en posterior mesenteriese arterieë is voorgestel as 'n veronderstelde sinapomorfie van cordylines + gerrhosaurines. Kenmerke van die lewerpoortsisteem is dalk outapomorfies vir die genus *Cordylus* of vir cordylines as geheel.

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Phylogenetic studies of lizards have traditionally focused on external and osteological characters. Soft characters have been employed only sporadically in reptilian systematics, partially because they are not always available for evaluation (as in analyses including fossils), but primarily because they are difficult and time consuming to examine. Circulatory and nervous patterns are especially difficult to trace in preserved material and frequently require extensive dissection and/or histological sectioning. Recently, however, a variety of techniques have been employed in morphological research that provide a more convenient analysis of these characters. Both the Sudan Black nerve stain (Filipski & Wilson 1985) and the Microfil™ injection technique (Russell, Bauer & Walker 1988; Russell, Walker & Bauer 1988) can be combined with clearing and staining of hard tissues to provide whole body mounts that retain positional information and can be easily examined. Other techniques for vascular visualization, such as the use of scanning electron microscopy of vascular corrosion casts are primarily effective at levels of circulatory hierarchy that tend to reflect functional rather than phylogenetic trends (see Discussion). In addition, such preparations require the complete maceration of all surrounding tissue (Christofferson & Nilsson 1988; Lametschwandtner, Lametschwandtner & Weiger 1990), thus making correlative studies of innervation and osteology impossible on single individuals.

Despite the difficulties inherent in visualizing the lizard circulatory system, a large body of comparative data on circulatory architecture has been accumulated. Zug (1971) provided a historical overview of the study of lizard arterial systems, and many of the works cited by him also reviewed the venous and hepatic portal systems of their respective study organisms. Research on morphology of vascular patterns in lizards has involved comparative studies of aorta and carotid arches (e.g. Rathke 1857; van Bemmelen 1886; Hochstetter 1901; de Silva 1956a; Adams 1957; Sidky 1967) as well as the visceral arteries and veins (e.g. Rathke 1863; Hochstetter 1892, 1898; Beddard 1904a, 1904b, 1906a, 1906b, 1907, Bhatia 1929; Mahendra 1942; Kashyap & Nigwekar 1964; Zug 1971). Although most of these studies were purely descriptive, some workers (e.g. Beddard 1904a, 1904b, 1906a, 1906b, 1907; Zug 1971) placed patterns of circulatory variation in a phylogenetic context. Representatives of most lizard groups have been examined with respect to vascular patterns, but the iguanian and gekkotan families, as well as varanids and lacertids, have received the greatest attention. Several families, however, have been treated only very superficially in general morphological works. One of the most species-rich families to be so neglected is the Cordylidae.

Cordylids are members of the scincomorphan clade of autarchoglossan lizards (Estes, de Queiroz & Gauthier 1988;

Presch 1988) and are probably the sister taxon of the Scincidae (Rieppel 1980; Estes et al. 1988; Lang 1991). There are approximately 71 species of cordylids in 10 genera distributed throughout much of sub-Saharan Africa and Madagascar. Two families, the Cordylidae *sensu stricto* and the Gerrhosauridae, have been recognized by some authors (e.g. FitzSimons 1943; Loveridge 1944; Lang 1991), but appear to be sister taxa of one another (Lang 1991) and are treated here as subfamilies. To date the only cordylids for which data on vasculature are available are *Chamaesaura anguina*, *Cordylus cordylus*, *Cordylus giganteus*, and *Gerrhosaurus flavigularis*. The first two taxa were included in Rathke's (1863) monograph on lizard and crocodilian arteries, the third was mentioned by Hochstetter (1898) and the last was the subject of a general anatomical paper by Beddard (1905). In addition, Hochstetter (1898) also briefly mentioned *Zonosaurus madagascariensis*, one of the taxa examined in the present study. Only Beddard (1905), however, provided details beyond the most basic patterns of the great vessels or made reference to the venous and hepatic portal systems.

In this paper we present a preliminary description of the vasculature, chiefly visceral, in two species of cordyline lizards and one species of gerrhosaurine in order to establish a baseline for future comparisons for potential systematic use within this group, and to identify intrafamilial variation that may subsequently serve as a source of characters for phylogenetic analysis.

Material and Methods

Two adult males of each of three cordylid taxa were used in the study. *Cordylus polyzonus* were collected at Jacobsbaai, Cape Province, Republic of South Africa, and *Cordylus jordani* were collected near Helmeringhausen, Republic of Namibia, under permits issued to the junior author. These species are sister taxa (Mouton 1986); the latter has even been considered a subspecies of the former by some authors (e.g. Loveridge 1944; Lang 1991). Two specimens of the Madagascan gerrhosaurine, *Zonosaurus madagascariensis* were obtained commercially in the United States.

Visualization of circulatory patterns was achieved by combining latex injection techniques with standard clearing and staining methods (Wassersug 1976). The injection method employed used the latex-based injection medium, Microfil™ (Canton Biomedical Products, Boulder, Colorado). Specimens were anesthetized with 10% T61 Euthanasia Solution (Hoechst Pharmaceuticals) and the dorsal aorta exposed by making a ventral abdominal incision and retracting the viscera. The dorsal aorta was cannulated bidirectionally with P.E. 50 tubing following the method of Russell *et al.* (1988a, b). Tubing was connected to two 10-ml syringes placed in parallel on a syringe pump. Specimens were exsanguinated by injecting heparinized saline at a flow rate of 0,1 ml/min until all blood had been flushed through a small puncture made in the pericardium and ventricular wall. Saline syringes were then replaced by syringes containing Microfil™ (MV 130, red; viscosity 110c mixed according to volume, using 5 parts diluent, 4 parts compound, and 5% by volume of curing agent). Infusion of Microfil™ followed the same procedure and flow rate as the heparinized saline, and was completed over a period of 10 min. Specimens were refrigerated for 24 h to ensure polymerization of the injection medium into an elastomeric gel.

Treated lizards were fixed in 10% neutral buffered formalin and cleared with trypsin and KOH and double-stained with alizarin red S and alcian blue (Wassersug 1976). Vascular patterns were examined with a Nikon SMZ-10 stereomicroscope. Patterns were mapped with the aid of a camera lucida and a microscope mounted 35 mm camera. The terminology employed generally follows that of O'Donoghue (1920), Mahendra (1942), Harris (1963), and Zug (1971), although Latin names have been anglicized. Commonly used synonyms for vessels are provided parenthetically at their first mention.

Results

The vascular branching patterns of *Cordylus polyzonus*, *Cordylus jordani*, and *Zonosaurus madagascariensis* are generally similar, with those of the first two taxa nearly identical. A general description of the circulatory pattern of *C. jordani* is presented and variations from this pattern in the other taxa are described. Discussion is chiefly limited to those vessels associated with the viscera.

Arterial system (Figure 1)

The most cranial branches of the aorta are three serial anterior gastric (esophageal) arteries, located immediately caudad of the union of the left and right systemic arches. These supply the anterior portion of the stomach and posterior region of the esophagus. A large coeliac artery supplies the mid- and posterior regions of the stomach, the spleen, and the pancreas through 6–7 major subbranches. Proximal-most with respect to the origin of the coeliac, a midgastric artery extends to the fundic region of the stomach and ramifies into a series of smaller vessels. In one of the specimens of *C. jordani* examined, a second midgastric branch was also present. A lienogastric artery arises next from the coeliac. This vessel bifurcates a short distance from its origin to form a lienic artery and a second midgastric artery. A second lienic artery and a posterior gastric artery originate more distally. The latter extends approximately to the midpoint of the greater curvature of the stomach where it sends off several short twigs as well as a longer branch which follows the curvature of the stomach anteriorly, terminating in the midgastric region. Distally, the coeliac bifurcates into a pancreatic artery and a second posterior gastric (pyloric) artery.

The second large, unpaired artery branching from the dorsal aorta is the posterior mesenteric or hepatomesenteric artery. This vessel gives rise to three major vessels supplying the liver, duodenum, posterior part of the small intestine, large intestine and colon. This vessel branches shortly after its origin from the dorsal aorta sending a hepatic artery anteriorly to supply the body of the liver. Approximately halfway between its origin and its entrance into the liver, the hepatic artery gives off a small duodenal artery. The posterior mesenteric artery bifurcates a short distance distal to the origin of the hepatic artery, near the junction of the large and small intestine. The more cranial of

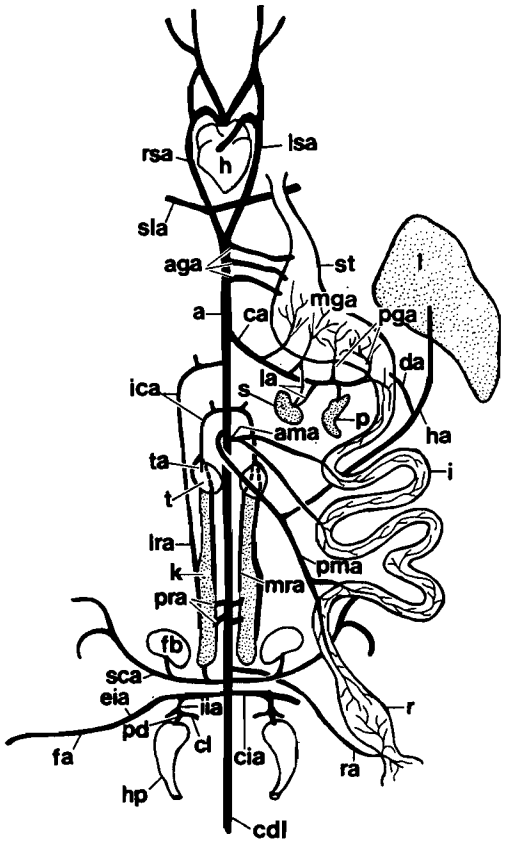

Figure 1 Diagrammatic ventral view of the postcardiac arterial system of *Cordylus jordani*. Abbreviations: a = aorta, aga = anterior gastric arteries, ama = anterior mesenteric artery, ca = coeliac artery, cdl = caudal artery, cia = common iliac artery, cl = cloacal artery, da = duodenal artery, eia = external iliac artery, fa = femoral artery, fb = fat body, h = heart, ha = hepatic artery, hp = hemipenis, i = intestine, ica = intercostal arteries, iia = internal iliac artery, k = kidney, l = liver, la = lienic arteries, lra = lateral renal artery, lsa = left systemic artery, mga = midgastric arteries, mra = medial renal artery, p = pancreas, pa = pancreatic arteries, pd = pudendal artery, pga = posterior gastric arteries, pma = posterior mesenteric artery, pra = posterior renal arteries, r = rectum, ra = rectal artery, rsa = right systemic artery, s = spleen, sca = sciatic artery, sla = subclavian artery, st = stomach, t = testis, ta = testicular artery

the branches thus formed supplies the posterior small intestine whereas the caudal branch or colonic artery supplies the large intestine. The anterior mesenteric artery, the origin of which is immediately caudal to that of the posterior mesenteric artery, is the third major visceral vessel. It bifurcates immediately after its origin, sending several branches throughout the length of the small intestines.

The testicular (spermatic) arteries, are thin, paired vessels branching from modified intercostal arteries posterior to the coeliac artery and anterior to the posterior mesenteric artery. The left modified intercostal artery branches from the aorta and splits into an intercostal branch supplying the body wall, and a branch supplying the urogenital system. Just above the level of the testis the left testicular artery branches from the most cranial of three renal arteries, which, in turn, is divided into a medial branch, paralleling the aorta and serving the anterior half of the kidney, and a lateral division supplying the midportion of the kidney. In the specimens examined the right renal artery remains undivided and enters the kidney only along the medial edge, whereas the lateral artery is derived from a modified intercostal artery of the preceding body segment.

Posterior to the major unpaired arteries are the second and third pairs of renal arteries, which branch symmetrically and supply the posterior region of the kidneys. An unpaired rectal artery originates from the aorta near the posterior margin of the kidneys, descending to the dorsal wall of the rectum. The next major branches from the dorsal aorta are a pair of sciatic (or pelvic) arteries, which extend to the abdominal fat bodies and pelvic musculature. The right and left arteries in one specimen of *C. jordani* vary slightly, with the right vessel giving off a small branch to the posterior portion of the right kidney in addition to its major divisions. The caudal-most of the paired arteries are the common iliacs, which branch into the external and internal iliac arteries. The former leads into the femoral artery, supplying the hindlimb, whereas the latter branches into a cloacal artery serving the cloacal wall and a pudendal artery supplying the hemipenis.

The arterial pattern of *Cordylus polyzonus* is identical to that of the *C. jordani* except with regard to the branching pattern of the coeliac artery and the origin of the anterior and posterior mesenteric arteries. In the former species there is no intermediate gastric artery between the second lienic artery and the terminal bifurcation of the coeliac. In *Cordylus polyzonus*, the posterior mesenteric artery and the anterior mesenteric artery arise simultaneously from the dorsal aorta, whereas the origin of the former is slightly cranial to that of the latter in *C. jordani*.

The architecture of the arterial system of *Zonosaurus madagascariensis* is generally similar to that of the *Cordylus* species examined but differs in several respects (Figure 2). The coeliac artery gives rise, in sequence, to an anterior gastric artery, a lienic artery, a midgastric artery, a pancreatic artery and a posterior gastric artery. The first of the posterior gastric arteries is short and supplies the posterior region of the stomach. The second consists of two branches, one extending on to the posterior-most part of the stomach, and the other to the greater curvature of the stomach,

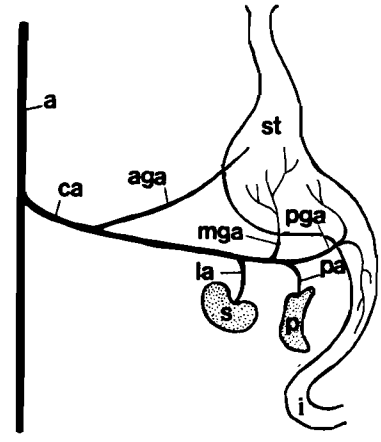

Figure 2 Diagrammatic view of the coeliac artery and its branches in *Zonosaurus madagascariensis*. Abbreviations as in Figure 1.

terminating in the midgastric region.

The testicular arteries originate from the dorsal aorta at a point intermediate between the coeliac artery and posterior mesenteric artery. However, whether these vessels originated directly from the dorsal aorta or from an intercostal artery could not be determined owing to poor filling by the injection medium at this junction. Three pairs of renal arteries, all of which originate directly from the aorta, are present in *Z. madagascariensis*.

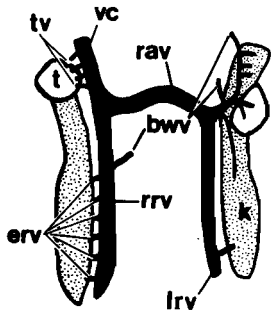

Figure 3 Diagrammatic ventral view of the renal portion of the venous system of *Cordylus jordani*. Abbreviations: bwv = body wall vein, erv = efferent renal veins, k = kidney, lrv = left renal vein, rav = renal anastomosing vein, rrv = right renal vein, t = testis, tv = testicular vein, vc = vena cava.

Venous system (Figure 3)

The pathway of venous return originates in a pair of renal veins that extend along the medial face of the kidneys. The right and left renal veins are asymmetrical, as is common in other lizards (Mahendra 1942). The right renal vein receives approximately six parallel efferent renal veins from the right kidney. In addition, it also receives a small vessel which collects blood from the dorsal body wall. The left renal vein, in addition to draining the posterior part of the kidney, receives a small vessel formed by the union of two testicular veins, one vein from the midregion of the kidney, and two branches from the body wall, one of which also receives three small efferent renal veins from the anterior region of the kidney. At approximately the level of the left testis the left renal vein angles to the right at almost 90° to its main axis to form the renal anastomosing vein, which joins the right renal vein to form the posterior vena cava. The right testis is drained by a series of testicular veins directly into the vena cava. Within the liver, the inferior vena cava receives a vertebral vein which has two main branches returning blood from the epaxial muscles of the trunk. The vena cava also receives a number of hepatic vessels which collect blood from the capillary networks of the liver, and prior to leaving this organ, collects blood from an esophageal vein, with four main divisions draining the esophagus and cardiac stomach.

No deviation from the *Cordylus jordani* pattern of venous architecture was noted in the major vessels of *C. polyzonus*, whereas in *Zonosaurus madagascariensis* the only difference noted was the presence of two esophageal veins.

Hepatic portal system (Figure 4)

The hepatic portal system receives blood from the gastrointestinal tract and transports it to the ventral lobe of the liver. Just within the tissue of the liver the visceral portion of the system is joined by the ventral abdominal vein, which drains the posterior somatic tissues. The caudal origin of the visceral portion of the hepatic portal system is the rectal vein. This vessel receives approximately 15 secondary vessels collecting blood from the colon and rectum. Slightly more anteriorly, the rectal vein receives the posterior intestinal vein from the large intestine to form the main portal trunk. More cranially, the portal vein receives, in sequence, the anterior intestinal vein, which is formed by the union of duodenal vein and several veins from the anterior and midsections of the small intestine, and the lienogastric vein, which collects venous flow from two lienic veins as well as from the mid- and posterior gastric regions via the pyloric vein. Two pancreatic veins enter the portal trunk independently, followed by the highly-branched posterior gastric vein, which collects blood from much of the stomach. The cranial-most vessel joining the hepatic

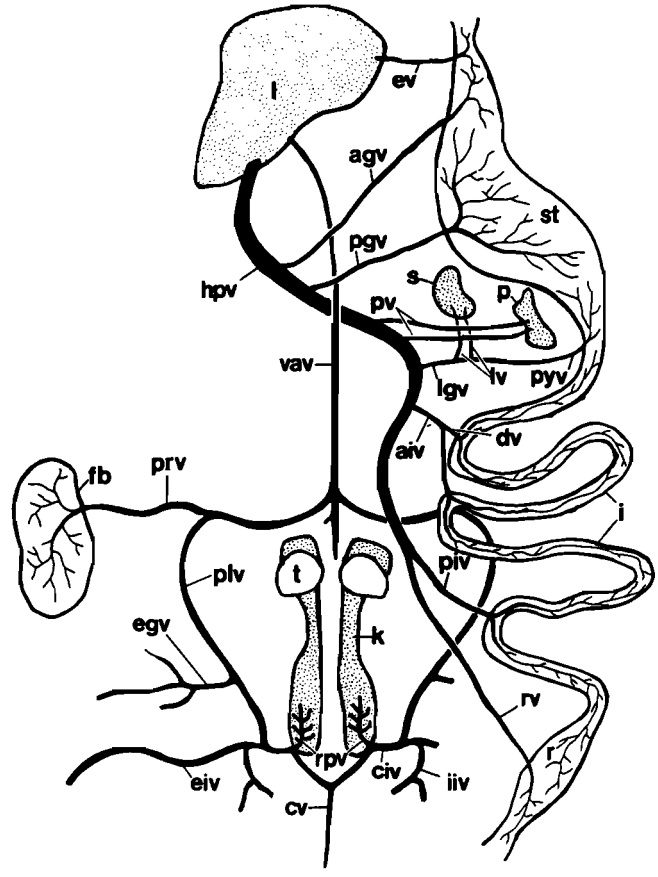

Figure 4 Diagrammatic ventral view of the hepatic portal system and abdominal drainage of *Cordylus jordani*. Abbreviations: agv = anterior gastric vein, aiv = anterior intestinal vein, civ = common iliac vein, cv = caudal vein, dv = duodenal vein, egv = epigastric vein, eiv = external iliac vein, ev = esophageal vein, fb = fat body, hpv = hepatic portal vein, i = intestine, iiv = internal iliac vein, k = kidney, l = liver, lgv = lienogastric vein, lv = lienic veins, p = pancreas, pgv = posterior gastric vein, piv = posterior intestinal vein, plv = pelvic vein, prv = parietal vein, pv = pancreatic veins, pyv = pyloric vein, r = rectum, rpv = renal portal veins, rv = rectal vein, s = spleen, st = stomach, t = testis, vav = ventral abdominal vein.

portal prior to its fusion with the ventral abdominal vein is the anterior gastric vein, which collects blood from the cardiac stomach. This vessel anastomoses with small vessels from the liver, close to the level of the esophageal vein.

The drainage of the ventral abdominal vein originates in the tail. After passing into the trunk, the caudal vein divides and gives rise to the renal portal veins, which ramify into afferent renal veins in the tissues of the kidney. Each renal portal vein is connected to the common iliac vein of the same side. The latter vessel is derived from the union of an internal iliac, draining the cloacal region and parts of the pelvic musculature, and an external iliac, draining the limb through its main branch, the femoral vein. Anastomosing with the common iliac near this division is a large pelvic vein. The left and right pelvic veins each pass anteriorly to fuse above the kidneys and gonads, forming the single ventral abdominal vein. Between the common iliac and ventral abdominal veins, each pelvic vein receives an epigastric vein and a large parietal vein draining the abdominal fat bodies and adjacent body wall.

No variation from this pattern was seen in *Cordylus polyzonus*, but significant differences were found in *Zonosaurus madagascariensis* (Figure 5). From posterior to anterior, the branches of the portal system in the latter species are: the rectal vein, a single intestinal vein, a lienic vein, a lienogastric vein, a pancreaticogastric vein and a large midgastric vein, similar in its tributary pattern to the posterior gastric vein of the cordylines. The last two of the portal branches in *Zonosaurus* branch immediately adjacent to one another. As in *Cordylus*, a branch of the gastric artery leads from the liver directly, in parallel with the esophageal veins.

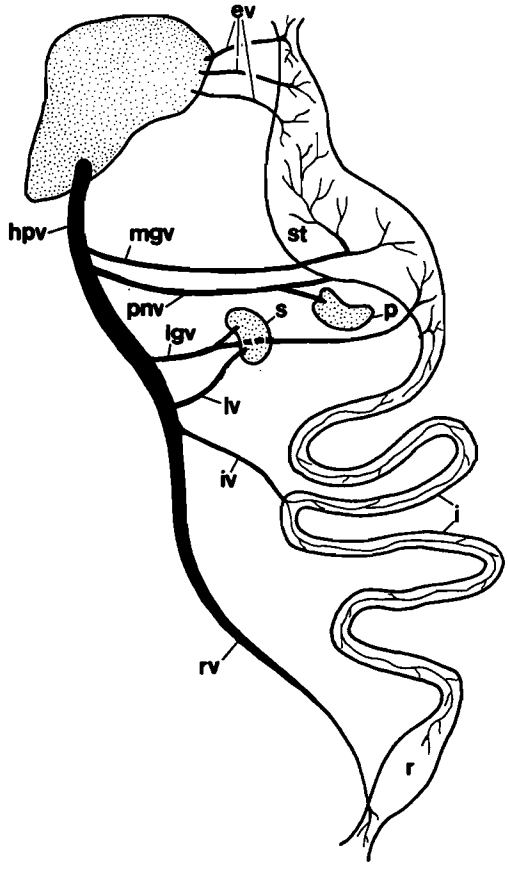

Figure 5 Diamgrammatic view of the hepatic portal system of *Zonosaurus madagascariensis*. Abbreviations as in Figure 4 except: iv = intestinal vein, mgv = midgastric vein, pnv = pancreaticogastric vein.

Discussion

Cordylus jordani, *Cordylus polyzonus*, and *Zonosaurus madagascariensis* exhibit a highly uniform venous pattern, moderate variation of arterial vessels and major differences in the hepatic portal system, particularly between the Cordylinae and Gerrhosaurinae. *Cordylus jordani* and *Cordylus polyzonus* are characteristically distinct from *Zonosaurus madagascariensis* in their possession of a double arterial supply to the spleen (Figures 1, 2) and in the possession of both anterior and posterior intestinal veins and a double portal drainage of the pancreas (as opposed to a single pancreaticogastric drainage; Figure 5).

Minor variation also occurs within the Cordylinae in the case of the origin of the anterior and posterior mesenteric arteries. *Zonosaurus madagascariensis* and *Cordylus jordani* share a condition not seen in *C. polyzonus*. In the first two species the posterior mesenteric artery arises slightly anterior to the anterior mesenteric artery, whereas in the last the two vessels arise at the same level. Such intrafamilial variation in the origin of the mesenteric arteries has been demonstrated to be a frequent occurrence in the Iguanidae, even within closely related groups of a subfamily (Zug 1971). Additional variations are suggested by the published reports of other cordylids examined: *Cordylus cordylus*, *Chamaesaura anguina* (Rathke 1863), *Cordylus giganteus* (Hochstetter 1898) and *Gerrhosaurus flavigularis* (Beddard 1905), but the data recorded are not strictly comparable with our own. Given the small sample of cordylid taxa that have been examined with respect to vasculature, it is not yet possible to evaluate the potential usefulness of circulatory patterns as sources of characters for use in intra-cordylid phylogenetics. Nonetheless, the greater similarity of *Cordylus* species to one another than to the gerrhosaurine *Zonosaurus* offers hope that at least some phylogenetic information may be resident in circulatory characters. Several features of the species of the *Cordylus* examined are putatively synapomorphic. The double hepatic drainage of the pancreas and the two lienic branches of the lienogastric vein are unique among all lizards for which data are available, and the pattern of dual arterial supply of the spleen is unknown in other scincomorphs. These features may provide additional support to the already robust hypothesis of cordyline monophyly (Lang 1991), or may be derived for some lower level within the hierarchy of the subfamily.

Comparative information is more abundant when interfamilial relations are considered. Although the position of cordylids relative to other lizard families is not entirely resolved (Estes *et al.* 1988; Presch 1988; Lang 1991), their inclusion within the Autarchoglossa, and Scincomorpha in particular, seems certain. Pending the polarization of vascular pattern characters on the basis of outgroup comparison, it may be of at least heuristic value to examine the cordylid condition in light of other lizards.

Rathke (1863) and Hocbstetter (1898) provided the most comprehensive basis for comparison of arterial patterns

among lizards. The anterior-most visceral arteries, the gastrics (referred to as esophageal arteries by some authors) lead directly from the aorta to the stomach and vary in number from one to nine among lizards (Rathke 1863; Beddard 1904b, 1905; Bhatia & Dayal 1933). Like cordylids, at least some gekkonids appear to have three anterior gastric arteries (Beddard 1904b). There seems to be no phylogenetically based pattern to the number of these vessels, except perhaps at low hierarchical levels. There may, however, be a functional correlation between an increased number of gastric arteries and the elongation of the viscera (Beddard 1904b, 1906a).

One of the most significant variations in the major vessels is the presence and order of branching from the aorta of the visceral arteries. Rathke (1863) outlined several major architectural plans of these vessels. The most widespread plan is characterized by the independent exit of unpaired coeliac, anterior mesenteric and posterior mesenteric arteries from the aorta. This is the pattern observed in the cordylids examined in this study as well as the cordylid taxa described by Rathke (1863) and Beddard (1905) and in most skinks. Patterns involving fusions of these vessels occur in a variety of lizards, including some agamids (Bhatia 1929), iguanids (Zug 1971) and lacertids and a few skinks (Rathke 1863). Among those forms possessing all three vessels, the most common sequence of branching from the aorta is: coeliac, posterior mesenteric, anterior mesenteric (Rathke 1863). In all cordylids examined the coeliac branching is substantially craniad to the mesenterics. Rathke (1863) reported that the origins of the two mesenterics in *Cordylus cordylus* were nearly at the same level with one another, and Hochstetter (1898) noted that the condition of the great vessels in *C. giganteus* was identical to that seen in *C. cordylus*. We also found this to be the case in the cordylids we examined, with simultaneous branching of the vessels in *C. polyzonus*. In *Gerrhosaurus flavigularis* these vessels are separated from one another by a single intercostal artery (Beddard 1905). This condition does not occur in *Chamaesaura*, but it may still stand as a putative synapomorphy of cordylids, with secondary variation in the grass lizards perhaps attributable to the constraints of elongation on visceral packing. Among other scincomorph lizards, the anterior and posterior mesenteric arteries originate very close to one another in representatives of the genera *Eumeces* and *Chalcides*, both scincine skinks.

Secondary branching of the coeliac artery is highly variable among lizards. Whereas most groups exhibit blood supply to the pancreas via the coeliac, as do cordylids, this is not the case in the agamid *Uromastyx* (Bhatia 1929; but see Thapar 1923). Another feature of the coeliac system, the arterial supply of the spleen, is variable within scincomorphs. In cordylines both lienic and lienogastric vessels supply the organ, whereas only the former is present in *Zonosaurus* and only the latter in the skink *Lygosoma guentheri* (Kashyap & Nigwekar 1964). In at least some other skinks, (e.g. *Scincus*) the spleen does receive two arteries, although both are primary branches of the coeliac artery.

Branching of the renal arteries anterior to the iliac and sciatic arteries is seen in *Lygosoma guentheri* (Kashyap & Nigwekar 1964) and *Chamaeleo chamaeleon* (Mackay 1886), as well as in the cordylids examined. In *Uromastyx* (Thapar 1923; Bhatia 1929) and *Hemidactylus flaviviridis* (Bhatia & Dayal 1933), however, renal arteries originate posteriorly of at least the sciatics. Both conditions have been reported for *Calotes versicolor* (de Silva 1956b; Paranjape 1974). Variation also exists in the origin of the sciatic arteries. Bhatia (1929) claimed that these vessels always arise as offshoots of the iliac arteries in lizards. This condition appears to be typical of agamids (Bhatia 1929; de Silva 1956b; Harris 1963; Paranjape 1974), but the independent derivation of these vessels from the aorta occurs in a range of scleroglossan lizards, including gekkotans (Bhatia & Dayal 1933), varanids (Thapar 1923) and the cordylids examined here. The derivation of the renals in common with intercostal arteries has previously been noted in another cordylid, *Gerrhosaurus flavigularis* (Beddard 1905) and in the anguid *Ophisaurus apodus* (Beddard 1906a).

Significant variation exists among lizards in the origin of the hepatic artery. In *Zonosaurus* and the two species of *Cordylus* examined in this study, the hepatic artery is a branch of the posterior mesenteric artery, as is the duodenal artery. Among taxa for which data are available, this pattern occurs elsewhere only among chameleons (Hochstetter 1898). The hepatic artery arises as a branch of the anterior mesenteric in some agamids (de Silva 1956b), and as a division of the coeliac in remaining lizards (Hochstetter 1898; Bhatia & Dayal 1933; Meinertz 1952). Likewise, in non-cordylids the duodenal artery is derived from the coeliac (scincids, Kashyap & Nigwekar 1964; agamids, de Silva 1956b), or two duodenal arteries are present, one each deriving from the coeliac and anterior mesenteric arteries (e.g. gekkonids, Bhatia & Dayal 1933). In *Ophisaurus* (Beddard 1906a) the liver is supplied by both a hepatic artery and a branch of the gastric artery.

The venous drainage of the viscera of lizards, as with cordylids in particular, shows little gross variation in pattern. The number of esophageal veins varies across lizards as a whole. A single vessel has been reported for *Hemidactylus flaviviridis* (Mahendra 1942) and *Varanus griseus* (Beddard 1904a), and two veins have been noted in skinks (Kashyap & Nigwekar 1964) and iguanids (Zug 1971). In other representatives of the Agamidae, Anguidae (Beddard 1906a) and Scincidae (Beddard 1904b) there are three veins which communicate directly from the anterior region of the stomach to the liver.

The greatest variation of the postcaval venous drainage occurs in the pattern of the renal veins and associated vessels. In the cordylids examined, only the left testicular veins drain into their respective renal vein, whereas the right testicular veins empty into the vena cava just craniad to the fusion of the left and right renals. In this regard the cordylid condition more closely resembles that of *Lacerta* (Hochstetter 1892), *Uromastyx* (Bhatia 1929), *Tiliqua* (Beddard 1904a), and *Lygosoma* (Kashyap & Nigwekar 1964), rather than the more symmetrical condition of *Varanus* (Thapar 1921; Bhattacharya 1921) and *Hemidactylus* (Mahendra 1942). As is typical for most lizards (Kashyap & Nigwekar 1964) the right renal vein of the cordylids is considerably shorter than the left, with which it fuses to form the posterior vena cava via the renal anastomosing vein (anterior transverse renal anastomosis). Mahendra (1942) identified

three major patterns of renal drainage among lizards. That characterized by the intrarenal origin of these vessels is seen in cordylids and has otherwise been recorded for lacertids (Hochstetter 1892), gekkonids (Mahendra 1942) and scincids (Kashyap & Nigwekar 1964).

Among lizards as a whole, as within the Cordylidae, hepatic portal drainage is highly variable. The double drainages from the pancreas in cordylines, and from the spleen in all three species examined, appear to be rare among lizards. Likewise, the presence of two large gastric veins (in cordylines) and a lienogastric connection from the stomach to the hepatic portal vein (all three species) is otherwise unknown. Only one gastric portal vein has been reported in *Hemidactylus flaviviridis* (Mahendra 1942), whereas *Lygosoma guentheri* exhibits a single such vessel divided relatively near its base (Kashyap & Nigwekar 1964). In *Iguana tuberculata* and *Tiliqua scincoides* a condition similar to that of *Zonosaurus* is found, with a single pancreaticogastric draining both the stomach and the pancreas (Beddard 1904b; Zug 1971). In *Pygopus* there are both a lienogastric vein and a separate lienic vein (Beddard 1904a). In *Tiliqua scincoides*, drainage of the spleen is achieved by a vessel that drains the small intestine as well (Beddard 1904b). In *Hemidactylus flaviviridis* there is a single intestinal vein and the pancreatic branch is caudal to the lienogastric (Mahendra 1942).

It is clear that there is extensive homoplasy in most vascular patterns among lizards. The variation of major vessel pattern, even among reasonably closely related taxa (Zug 1971) has lead to the hypothesis that no one pattern is mechanically more efficient than another (Iberall 1967), because many patterns can accommodate nearly identical vessel cross-sectional areas, and therefore comparable blood pressures. As a result, there appears to be little constraint, either phylogenetically or functionally, acting to restrict variation in circulatory architecture. Indeed, Rathke (1863) found extensive variation in some aspects of arterial pattern in a sample of 10 specimens of *Anguis fragilis* and other authors have noted intraspecific variations of a lesser nature.

Zug (1971) found relatively little congruence among iguanids between patterns suggested by arterial architecture and those derived from osteological and other characters. Interfamilial vascular patterns among lizards are even more difficult to interpret. Some of the confusion may reflect artifact, as in the case of *Calotes versicolor*, in which rather dissimilar arterial patterns have been described by different authors (de Silva 1956b; Paranjape 1974). It is difficult to ascertain whether such apparent differences reflect intraspecific variation or misinterpretation.

Nonetheless, some vascular characters do appear to reflect phylogeny. It is perhaps significant that scincids share with cordylids the anterior position of the renal arteries, the asymmetry of the gonadal arteries and a similar drainage pattern of the kidneys. Unfortunately, none of these characters can be assigned polarity and determination of the plesiomorphic, apomorphic or homoplastic nature of their shared occurrence must await a more thorough analysis of vessel patterns in lizards. Evidence from other autarchoglossans, in particular, may provide additional data to distinguish between alternative hypotheses of relationship in which cordylids are the sister group of the Scincidae (Rieppel 1980; Estes *et al.* 1988; Lang 1991) or of the Scincidae + Xantusiidae (Presch 1988).

The two most recent phylogenetic analyses incorporating all scincomorph lizards (Estes *et al.* 1988; Presch 1988) each used only a single vascular character, and the only study of relationships within cordylids (Lang 1991) used none. The results of this study suggest that some characters, such as the relative position of the anterior and posterior mesenteric arteries may be useful in diagnosing the Cordylidae as a whole. Lang (1991) found little support for the monophyly of the family from osteology. The reality of the group rests on a few characters from karyology (Olmo & Odierna 1980), myology (Rieppel 1980) and hemipenial morphology (Böhme 1988). Confirmation of the evolution of the putatively synapomorphic mesenteric arterial character at the base of the cordylid clade would be corroborative.

At lower hierarchical levels, vascular characters may be useful in evaluating the existing, robust hypothesis of intrageneric relationships within the Cordylinae and Gerrhosaurinae (Lang 1991) and in contributing to data sets pertinent to interspecific patterns of relationship, which have been limited to date (e.g. Mouton 1986). Verification of the systematic value of these characters and the effective utilization of others will require the collection of comparative data from both a wider range of cordylids (in order to assess in-group character state distributions), and a diversity of lizards in other autarchoglossan families (in order to assess character state polarity relative to the Cordylidae).

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References

ADAMS, W.E. 1957. The carotid bifurcation in *Chamaeleo*. *Anat. Rec.* 128: 651–660.

BEDDARD, F.E. 1904a. Contributions to the anatomy of the Lacertilia. (1) On the venous system in certain lizards. *Proc. Zool. Soc. London* 1904(1): 436–450.

BEDDARD, F.E. 1904b. Contributions to the anatomy of the Lacertilia. (3) On some points in the vascular system of *Chamaeleon* and other lizards. *Proc. Zool. Soc. London* 1904(2): 6–22.

BEDDARD, F.E. 1905. Some notes on the anatomy of the yellow-throated lizard, *Gerrhosaurus flavigularis*. *Proc. Zool. Soc. London* 1905(2): 256–267.

BEDDARD, F.E. 1906a. Some additions to the knowledge of the anatomy, principally of the vascular system, of *Hatteria*, *Crocodilus*, and certain Lacertilia. *Proc. Zool. Soc. London* 1905(2): 461–489.

BEDDARD, F.E. 1906b. On the vascular system of *Heloderma*, with notes on that of the monitors and crocodiles. *Proc. Zool. Soc. London* 1906(2): 601–625.

BEDDARD, F.E. 1907. Contributions to the knowledge of the systematic arrangement and anatomy of certain genera and species of Squamata. *Proc. Zool. Soc. London* 1907: 35–68.

BHATIA, M.L. 1929. On the arterial system of the lizard *Uromastix hardwickii* Gray. *J. Morphol. Physiol.* 48: 281–316.

BHATIA, M.L. & DAYAL, J. 1933. On the arterial system of the lizard *Hemidactylus flaviviridis* Rüppel. *Anat. Anz.* 76: 417–437.

BHATTACHARYA, D.R. 1921. Notes on the venous system of *Varanus bengalensis*. *J. Proc. Asiat. Soc. Bengal (n.s.)* 17: 251–261.

BÖHME, W. 1988. Zur Genitalmorphologie der Sauria: funktionelle und stammesgeschichtliche Aspekte. *Bonn. Zool. Monogr.* 27: 1–176.

CHRISTOFFERSON, R.H. & NILSSON, B.O. 1988. Microvascular corrosion casting with analysis in the scanning electron microscope. *Scanning* 10: 43–63.

DE SILVA, P.H.D. 1956a. The arterial system of *Calotes versicolor* (Daudin) with notes upon the arterial system of *Calotes calotes* (Linne) and *Calotes nigrilabris* Peters. *Spol. Zeyl.* 28: 55–67.

DE SILVA, P.H.D. 1956b. The heart and aortic arches in *Calotes versicolor* (Daudin) with notes upon the heart and aortic arches in *Calotes calotes* (Linne) and *Calotes nigrilabris* Peters. *Spol. Zeyl.* 28: 68–86. [Note that the titles of DE SILVA 1956a and 1956b are transposed relative to the contents of the papers.]

ESTES, R., DE QUEIROZ, K. & GAUTHIER, J. 1988. Phylogenetic relationships within Squamata. In: Phylogenetic relationships of the lizard families, Essays Commemorating Charles L. Camp. (Eds.) R. Estes & G. Pregill, pp. 119–181. Stanford University Press, Stanford, California.

FILIPSKI, G.T. & WILSON, M.V.H. 1985. Staining nerves in whole cleared amphibians and reptiles using Sudan Black B. *Copeia* 1985: 500–502.

FITZSIMONS, V.F. 1943. The lizards of South Africa. *Mem. Transvaal Mus.* 1: i–xv, 1–527 + 24 pls. + map.

HARRIS, V.A. 1963. The anatomy of the rainbow lizard. Hutchinson & Co., London.

HOCHSTETTER, F. 1892. Beiträge zur Entwicklungsgeschichte des Venensystems der Amnioten. II. Reptilien (*Lacerta, Tropidonotus*). *Gegenbaurs Morphol. Jb.* 19: 428–501 + pls. 15–17.

HOCHSTETTER, F. 1898. Über die Arterien des Darmkanals der Saurier. *Gegenbaurs Morphol. Jb.* 26: 213–273 + pls. 5–7.

HOCHSTETTER, F. 1901. Über Varietäten der Aortenbogen, Aortenwurzeln und der von ihnen entspringenden Arterien bei Reptilien. *Gegenbaurs Morphol. Jb.* 29: 415–438 + pl. 24.

IBERALL, A.S. 1967. Anatomy and steady flow characteristics of the arterial system with an introduction to its pulsatile characteristics. *Math. Biosci.* 1: 375–395.

KASHYAP, H.V. & NIGWEKAR, V.B. 1964. The blood vascular system of *Riopa guentheri* (Peters) Reptilia: Sauria. *Proc. Indian Acad. Sci.* 59: 195–210.

LAMETSCHWANDTNER, A., LAMETSCHWANDTNER, U. & WEIGER, T. 1990. Scanning electron microscopy of vascular corrosion casts — technique and applications: updated review. *Scanning Electron Microsc.* 4: 889–941.

LANG, M. 1991. Generic relationships within cordyliformes (Reptilia: Squamata). *Bull. Inst. Roy. Sci. Nat. Belg.* 61: 121–188.

LOVERIDGE, A. 1944. Revision of the African lizards of the family Cordylidae. *Bull. Mus. Comp. Zool.* 95: 1–118 + 12 pls.

MACKAY, J.Y. 1886. The arterial system of the chamaeleon (*Chamaeleo vulgaris*). *Proc. Phil. Soc. Glasgow.* 17: 353–356.

MAHENDRA, B.C. 1942. Contributions to the bionomics, anatomy, reproduction and development of the Indian house-gecko, *Hemidactylus flaviviridis* Rüppel. Part III. The heart and the venous system. *Proc. Indian Acad. Sci.* 15B: 231–252.

MEINERTZ, T. 1952. Das Herz und die grossen Blutgefässe bei der Komodoeidechse, *Placovaranus komodoensis* Ouw. *Z. Anat. Entwicklunges* 116: 315–325.

MOUTON, P. le F.-N. 1986. Description of a new species of *Cordylus* Laurenti (Reptilia: Cordylidae) from the south-western Cape, South Africa. *S. Afr. J. Zool.* 21: 319–324.

O'DONOGHUE, C.H. 1920. The blood vascular system of the tuatara, *Sphenodon punctatus*. *Phil. Trans. Roy. Soc. London* 210B: 175–252.

OLMO, E. & ODIERNA, G. 1980. Chromosomal evolution and DNA of cordylid lizards. *Herpetologica* 36: 311–316.

PARANJAPE, S.Y. 1974. The anatomy of the garden lizard. University of Poona Press, Poona, India.

PRESCH, W. 1988. Cladistic relationships within the Scincomorpha. Phylogenetic relationships of the lizard families. Essays commemorating Charles L. Camp. (Eds.) R. Estes & G. Pregill, pp. 471–492. Stanford University Press, Stanford, California.

RATHKE, H. 1857. Untersuchungen über die Aortenwurzeln und die von ihnen ausgehenden Arterien der Saurier. *Denkschr. kaiserl. Akad. Wiss. Math. Naturwiss. Cl.* 13: 51–142 + pls. 1–6.

RATHKE, H. 1863. Untersuchungen über die Arterien der Verdauungswerkzeuge der Saurier. *Abh. Mat.-Phys. Cl. Königl. Bayer. Akad. Wiss.* 9: 127–183.

RIEPPEL, O. 1980. The trigeminal adductor musculature of *Tupinambis*, with comments on the phylogenetic relationships of the Teiidae (Reptilia, Lacertilia). *Zool. J. Linn. Soc.* 69: 1–29.

RUSSELL, A.P., BAUER, A.M. & WALKER, R.L. 1988. A technique for visualization of the circulatory system in small lizards. *Copeia* 1988: 797–800.

RUSSELL, A.P., WALKER, R.L. & BAUER, A.M. 1988. Microfil™ injections of small vertebrates: an adjunct to clearing and staining. *Coll. Forum* 3: 3–5.

SIDKY, Y.A. 1967. The carotid sinus in lizards with an anatomical survey of the ventral neck region. *J. Morphol.* 121: 311–322.

THAPAR, G.S. 1921. On the venous system of the lizard *Varanus bengalensis* (Daud.). *Proc. Zool. Soc. London* 1921: 487–492.

THAPAR, G.S. 1923. On the arterial system of the lizard *Varanus bengalensis* (Daud.) with notes on *Uromastix* and

Hemidactylus. *J. Asiat. Soc. Bengal (n.s.)* 19: 1–13.

VAN BEMMELEN, J.F. 1886. Die Visceralten und Aorten bei Reptilien und Vögeln. *Zool. Anz.* 9: 528–532.

WASSERSUG, R.J. 1976. A procedure for differential staining of cartilage and bone in whole formalin fixed vertebrates. *Stain Technol.* 51: 131–134.

ZUG, G. 1971. The distribution and patterns of the major arteries of the iguanids and comments on the intergeneric relationships of iguanids (Reptilia: Lacertilia). *Smithson. Contrib. Zool.* 83: 1–22.